DID BOWHEAD WHALES (*BALAENA MYSTICETUS*) FROM THE BERING-CHUKCHI-BEAUFORT SEAS UNDERGO A GENETIC BOTTLENECK? A TEST USING NUCLEAR MICROSATELLITE LOCI

A Thesis

by

DEVRA DENISE HUNTER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2005

Major Subject: Wildlife and Fisheries Sciences

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Committee Members,	Rodney L. Honeycutt
	Robert A. Wharton
Head of Department,	Robert D. Brown

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ABSTRACT

Did Bowhead Whales (*Balaena mysticetus*) from the Bering-Chukchi-Beaufort Seas Undergo a Genetic Bottleneck? A Test Using Nuclear Microsatellite Loci.

(August 2005)

Devra Denise Hunter, B.S., Texas A&M University

Chair of Advisory Committee: Dr. John W. Bickham

This study reexamines the nuclear microsatellite analysis by Rooney et al. (1999a) of Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*) to determine if this population underwent a genetic bottleneck as a result of 19th and early 20th Century commercial whaling. This investigation used more accurate laboratory techniques to score alleles, had a larger sample size that was divided into two groups (mainland Alaska and St. Lawrence Island (SLI)), and used a moderately different set of microsatellite loci which are more variable and thus, more informative. The results corroborate the findings of Rooney et al. (1999a) for mainland Alaska showing no evidence of a genetic bottleneck. However, the SLI data analyses provide conflicting conclusions. The Wilcoxon test is significant for a heterozygote excess ($p = 0.042$) suggesting that a genetic bottleneck has occurred. This is not substantiated by the exact tests of each locus or the table-wide sign test. There is a possibility that a bottleneck has occurred, but due to the small sample size this is not a definitive conclusion and warrants reanalysis with a larger sample size.

DEDICATION

Without the support of my family I could never have completed this endeavor. I dedicate this work to my parents in response to their unconditional encouragement. They were always there when life got overwhelming. And to my best fluffy friends: Spooky, Gretchen, Miss Priss, and Becca whose nights were often interrupted by my obsessive behavior and who endured sporadic and intense attention or lack thereof.

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Thanks to the Alaska Eskimo Whaling Commission (AEWC) and the Barrow Whaling Captains' Association for their confidence, guidance and support of our research. The postmortem examinations that were conducted on landed whales often interfere with the butchering process. The whale hunters' patience has been enormous.

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Dr. John C. Patton supplied immeasurable assistance in the genetics lab from the stage of raw tissue to final allele calls. Additional technical and analytical support was provided by Dr. Cole W. Matson and Dr. April Harlin.

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INTRODUCTION

Classification and Distribution

The bowhead whale, *Balaena mysticetus*, is a mysticete cetacean in the family Balaenidae. The common name, bowhead whale, is derived from its large, bow-shaped skull that is greater than 5 meters long (Montague 1993). This species has also been referred to as the arctic whale, arctic right whale, black right whale, cisarctic right whale, common whale, great polar whale, Greenland whale, Greenland right whale, polar whale, right whale, or whalebone whale (Montague 1993). Unlike other whales, bowheads are restricted in distribution to cold arctic waters. Their epidermis can be up to 2.4 mm in thickness and the blubber layer up to 28 cm (Haldiman and Tarpley 1993). Several features of the bowhead, including its thick layer of "maktak" (blubber and skin) coupled with low surface area to body volume ratio, allow bowheads to occupy the waters of the Beaufort and Chukchi Seas that average temperatures below 0˚C (Brower et al. 1988).

Bowheads have a circumarctic distribution, and as such, their range has shifted drastically over the last 10,500 years with the movement of polar ice (Dyke et al. 1996). Currently, there are five recognized stocks of bowhead whales: Bering-Chukchi-Beaufort Seas (BCB), Okhotsk Sea, Davis Strait, Hudson Bay, and Spitsbergen stocks (Moore and Reeves 1993). The BCB stock is the largest with an estimated 10,545 animals (Zeh and Punt 2004).

This thesis follows the style and format of the Journal of Mammalogy.

The bowhead whale has been a prey item of humans for approximately 3,800 years, as documented from Cape Krusenstern, Alaska (Giddings 1967). The first commercial whaling of bowheads was implemented by Basques near Labrador, Canada, prior to 1547 and lasted between 50 and 100 years. Bowhead whale populations were subject to severe hunting pressures in the late 1800's and early 1900's by commercial whaling (Montague 1993). This led to their initial protection by the League of Nations Convention in 1931. Later in 1935, all whales in the family Balaenidae were protected by United States law. Hunting was banned except by aboriginal people for personal consumption. The International Whaling Commission (IWC), formed in 1946 by the International Convention for the Regulation of Whaling, regulates the bowhead whale aboriginal harvest.

Currently, the only peoples actively hunting whales in the BCB stock are Inuits. They hunt via a quota system under the auspices of the IWC, recognizing the cultural and nutritional aspects of the hunt. This is strictly a subsistence harvest and is closely monitored and regulated through a Cooperative Agreement between National Oceanic and Atmospheric Administration (NOAA) and the Alaska Eskimo Whaling Commission (AEWC).

Prior to the moratorium on whaling, severe hunting pressure from commercial whaling caused a decline in the size of all bowhead whale populations. Pre-whaling BCB population estimates are 15,000 individuals (Givens et al. 1995). Woodby and Botkin (1993) estimated that this population consisted of only 1,000 animals at its lowest point in history (93.3% reduction). Given this drastic reduction in whale numbers and

the fact that the exact number to which the population declined is not known for certain, there is concern that a genetic bottleneck occurred during the whaling era. A genetic bottleneck is defined as a reduction in population size that leads to increased genetic drift, with the concomitant loss of genetic diversity resulting in a decreased ability of the population to adapt to changing environmental conditions. These factors increase the probability of extinction and thus the conservation of genetic diversity has become a cornerstone of modern conservation biology (Beardmore 1983). Currently, the BCB stock is estimated to be sustaining an annual increase of 3.4% (George et al. 2004). Despite this increase, there is still concern over levels of genetic variability in the species.

This study utilizes microsatellite loci to estimate levels of genetic diversity in bowhead whales. These genetic markers have proven useful in previous studies of cetaceans (Amos et al. 1993, Richard et al. 1996, Valsecchi et al. 1997). Microsatellite loci are segments of DNA composed of di-, tri- or tetra-nucleotide repeats. Alleles differ in the number of times the repeated segment occurs. Because of their high levels of polymorphism and rather high rates of mutation, microsatellite loci are ideal markers for evaluating genetic effects of bottlenecks (Houlden et al. 1996).

Two methods to detect recent bottlenecks include the use of allele frequency data and heterozygosity (Luikart et al. 1998b, Piry et al. 1999). For a population in Hardy-Weinberg equilibrium, expected and observed heterozygosities are equal, whereas a bottlenecked population will exhibit excess heterozygosity. This results from the rapid

loss of rare alleles and a resultant decrease in expected levels of heterozygosity (Hedrick et al. 1986, Luikart and Cornuet 1998a).

Rooney et al. (1999a) used 20 microsatellite loci, 15 of which were variable, to evaluate genetic variation in bowhead whales from the BCB stock. They observed no heterozygosity excess and allele frequency distributions were normal. Thus, they indicated a lack of evidence supporting a genetic bottleneck in the BCB stock. This study differs from that of Rooney et al. (1999a) in several ways. First, PCR (polymerase chain reaction) products were analyzed on an autosequencer using fluorescence-labeled primers instead of radioactively labeled products scored visually from autoradiographs. Second, the selection of loci differed in that loci were chosen based on presence of variability and likeliness to be informative. Nine loci were in common with Rooney et al. (1999a) with 3 additional loci (GATA28, EV01, and EV104) added on the basis of findings from other studies (LeDuc et al. 1998, MacLean 2002). Third, Rooney et al. (1999) combined all into a single population, whereas I considered 2 groups for analysis (mainland Alaska and St. Lawrence Island) based on the findings of Givens et al. (2004) that revealed potential genetic subdivision in the BCB stock. Finally, this study builds on the work of Rooney et al. (1999a) with a larger sample size in an attempt to reexamine evidence for a potential genetic bottleneck of bowhead whales in the BCB stock. The primary objective of this study was to determine whether the severe reduction in population size of bowhead whales during the commercial whaling period significantly reduced genetic variability of the species.

METHODS

Study Area and Sample Size

Tissue samples were obtained from 201 bowhead whales from the BCB stock. All samples were provided by scientists from the North Slope Borough or native hunters. Those collected by hunters were obtained from 5 Alaskan mainland villages (Barrow, Kaktovik, Nuiqsut, Point Hope, and Wainright) and 2 villages on St. Lawrence Island (Gambell and Savoonga) (Fig. 1). Samples included tissues (skin and underlying blubber) obtained from villages where hunts originated (Table 1). Samples were collected from animals harvested according to catch limits determined by the IWC. Animals from Nuiqsut, an unlabeled sample, and 3 Barrow samples are from strandings.

Table 1. Sample sizes and localities for bowhead whales used in this study.

Village	Total Samples	Final Dataset
Barrow, Alaska	177	141
Gambell, St. Lawrence Island, Alaska	4	4
Kaktovik, Alaska	6	2
Nuiqsut, Alaska	1	-
Point Hope, Alaska	3	3
Savoonga, St. Lawrence Island, Alaska	7	6
Wainwright, Alaska	2	2
Unknown	1	-
Total	201	158

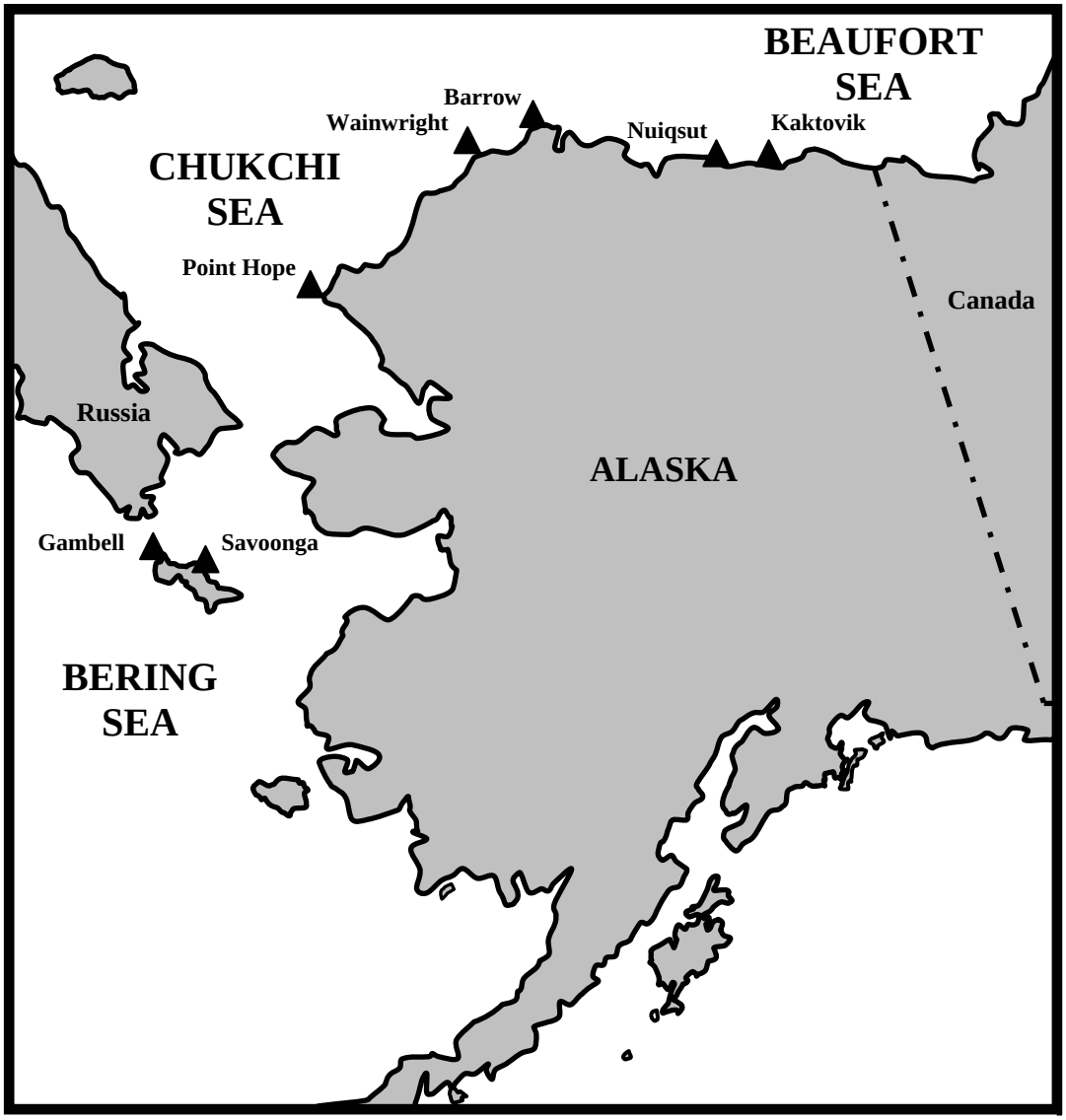

Fig. 1. Map illustrating sample collection sites for *Balaena mysticetus* collected for this study.

Molecular Methods

Tissues were preserved in a DMSO/NaCl solution, and all collection information and associated data were entered into a Microsoft Access database. Samples were subsequently stored at -80^{o} C. DNA was extracted from tissues using a modified

phenol-chloroform protocol (Maniatis et al. 1982). A precipitation using a Puregene protein solution (Gentra Systems, Minneapolis, Minnesota) along with sodium chloride was performed before the extraction. Quick-Precip (Edge Biosystems, Gaithersburg, Maryland) was added in conjunction with ethanol to aid in DNA precipitation after the organic extraction. These steps removed impurities (e.g., melanin) that impede DNA replication. Amount of extracted genomic DNA for each sample was quantified by electrophoresis on a 3.0% agarose gel using a 1 kb DNA ladder (New England Biolabs, Beverly, Massachusetts) as a size standard. Gels were stained with propidium iodide and visualized on an Eagle Eye II (Strategene, LaJolla, California). This genomic DNA provided a template for PCR amplification of 12 microsatellite loci (Table 2). Amplifications were performed on a GeneAmp PCR System 2700 (Applied Biosystems, Foster City, California). Detailed information for all loci is described in Table 2. PCR reactions consisted of 1.0 µL of template DNA, 0.1 µL of *Taq* polymerase, 7.9 µL distilled water, and 1.5 µL 10X *Taq* salts, 8 mM dNTP mix, forward (fluorescent labeled) and reverse primers. Amplifications were performed in 15µL volumes for 36 cycles under the following conditions: denaturation at 95°C for 20 seconds, annealing at variable temperatures (primer dependant, Table 2) for 15 seconds, and extension at 72°C for 30 seconds. Amplification products were visualized on an Eagle Eye II (Strategene) for a rough quantification. The product was then mixed with a size standard (400 Rox) and analyzed on an ABI Prism 377 DNA Sequencer (Applied Biosystems) using Genescan® Analysis v. 3.1.2. Four to 5 non-overlapping loci were analyzed on the same gel run. Allele calls were made by the author and questionable calls were rerun after re-

amplification. Allele sizes were estimated using the program Genotyper® v. 2.5. All calls were confirmed by Dr. John C. Patton.

Table 2. Descriptions and summary data for microsatellite loci used in analysis of *Balaena mysticetus.*

Locus	Label	Repeat Sequence	T_a(ºC)	k_o	Size Range (bp)
TV7[a]	6-FAM	$(CA)_{12}$	59	15	147 – 193
TV11[b]	HEX	$(TG)_{14}$	59	5	239 – 247
TV13[b]	FAM	$(TG)_{13}$	66	7	295 – 309
TV14[b]	HEX	$(TG)_{16}$	52	8	93 – 107
TV16[b]	6-FAM	$(CA)_{10}$	60	4	184 – 192
TV17[b]	FAM	$(TC)_4TGTAAAATATTTA(CA)_{22}$	52	11	189 – 211
TV18[b]	HEX	$(TG)_{14}$	50	7	73 – 85
TV19[b]	HEX	$(CA)_6GA(CA)_{21}$	62	6	172 – 182
TV20[b]	NED	$(TG)_{15}$	60	6	156 – 172
GATA28[c]	NED	$(GATA)_{28}$	52	10	115 – 182
EV1[d]	HEX	$(AC)_{13}(TC)_8$	56	6	135 - 147
EV104[d]	6-FAM	$(AC)_{14}(GCAC)_2$	54	11	140 – 160

[a] Rooney et al. 1999b
[b] Rooney et al. 1999a
[c] Palsbøll et al. 1997
[d] Valsecchi and Amos 1996
T_a annealing temperature
k_o number of alleles observed

Statistical Methods

Allelic data were analyzed using the program BOTTLENECK v. 1.2.02 (Cornuet and Luikart 1996). The data were split into 2 groups, mainland Alaska and St. Lawrence Island animals. The Alaska/SLI separation was based on preliminary findings that suggested the possibility of 2 potentially distinct genetic groups (Givens et al. 2004). Additionally, the locus TV18 was excluded from the final analyses because of problems that appear to be a non-biological consequence of the PCR process. A correlation

between allele size and heterozygote deficiency was revealed indicating short allele dominance (Jorde et al. 2004).

Three mutation models have been developed to explain the evolution of microsatellites: Infinite Alleles Model (IAM), Two Phase Model (TPM), and Stepwise Mutation Model (SMM). The IAM results in completely new alleles that did not previously exist (Kimura and Crow 1964), whereas the SMM assumes that mutations occur by one step forward or backwards, thus allowing for reverse mutations to existing states (Chakraborty and Nei 1977, Cornuet and Luikart 1996, Piry et al. 1999). As both the IAM and SMM are extremes, neither is likely to be optimal for all datasets (Cornuet and Luikart 1996). Therefore, I applied the TPM, which is an intermediate model that employs both models. This evolutionary model accommodates for variance in homogeneity across all loci and is most likely to occur in nature (Primmer et al. 1998, Estoup and Cornuet 2000). Estimates were based on the maximum number of replications allowed (10,000). Standardized difference was calculated for each individual locus to determine if any loci exhibit a significant heterozygosity deficiency or excess (Cornuet and Luikart 1996). A sign test and Wilcoxon rank test were performed to determine if there is a pattern of heterozygosity deficiency or excess across all loci (table-wide effect) in the dataset (Cornuet and Luikart 1996).

Finally, using BOTTLENECK, a mode shift test was performed to analyze the frequency distributions of the alleles. This is a graphical method to detect a recently bottlenecked population. Alleles are grouped in the following frequency classes: 1 low frequency (0-0.100), 8 intermediate frequencies (0.101-0.900), and 1 high frequency

(0.901-1.00). If there are less alleles in the low frequency class than in 1 or more intermediate frequency classes, the population is determined to have experienced a bottleneck and will drift away from the normal L-shaped allele frequency distribution (Luikart et al. 1998b). The assumptions of this test are that the population is randomly mating, there is no substock structure, loci are selectively neutral, and the individuals were randomly selected (Luikart et al. 1998b).

RESULTS

Allelic data from mainland Alaska (Table 3) and SLI (Table 4) were analyzed using BOTTLENECK. In the Alaskan mainland samples, 3 loci showed deviation from expected values of heterozygosity. TV19 and GATA28 had significant heterozygosity excesses and TV7 had a significant heterozygosity deficiency. For SLI samples, no loci showed significant deviations from expected values (Table 4).

Based upon a table-wide sign test, neither population (Alaska mainland, p = 0.105; SLI, p = 0.276) showed significant heterozygosity excess or deficiency. The Wilcoxon test also revealed no significant effects for the Alaska mainland population (one-tailed test for heterozygosity excess p = 0.087; one-tailed test for heterozygosity deficiency p = 0.926; two-tailed test p = 0.174).

The SLI population revealed significant heterozygosity excess (p = 0.042) based on the Wilcoxon test. Consequently, there was no significant probability of heterozygosity deficiency (p = 0.966). However, the two-tailed test was nonsignificant (p = 0.083). The sign test revealed no evidence of a genetic bottleneck (p = 0.277). Both populations showed an L-shaped allele frequency distribution with the mode shift test (Fig. 2, Fig. 3) indicative of a non-bottlenecked population.

Table 3. Mainland Alaska BOTTLENECK data.

	Observed			Under TPM		
Locus	n	k_o	H_o	H_e	$(H_o-H_e)/SD$	Probability
TV7	288	14	0.687	0.831	-3.156	**0.0138**
TV11	282	5	0.604	0.547	0.414	0.4098
TV13	294	7	0.695	0.661	0.328	0.4477
TV14	294	8	0.638	0.700	-0.690	0.2014
TV16	296	4	0.465	0.461	0.025	0.4235
TV17	260	10	0.808	0.762	0.645	0.2852
TV19	252	6	0.788	0.612	1.442	**0.0113**
TV20	296	6	0.656	0.608	0.395	0.4212
GATA28	296	10	0.867	0.760	1.5185	**0.0051**
EV1	270	6	0.754	0.612	1.164	0.0703
EV104	282	10	0.837	0.762	1.081	0.0937

n sample size (haploid genomes)
k_o number of alleles observed
H_o observed heterozygosity
H_e expected heterozygosity
SD standard deviation

* Positive $(H_o-H_e)/SD$ values indicate a heterozygosity excess, negative values identify a deficiency

** Significant p-values shown in bold ($p \leq 0.05$)

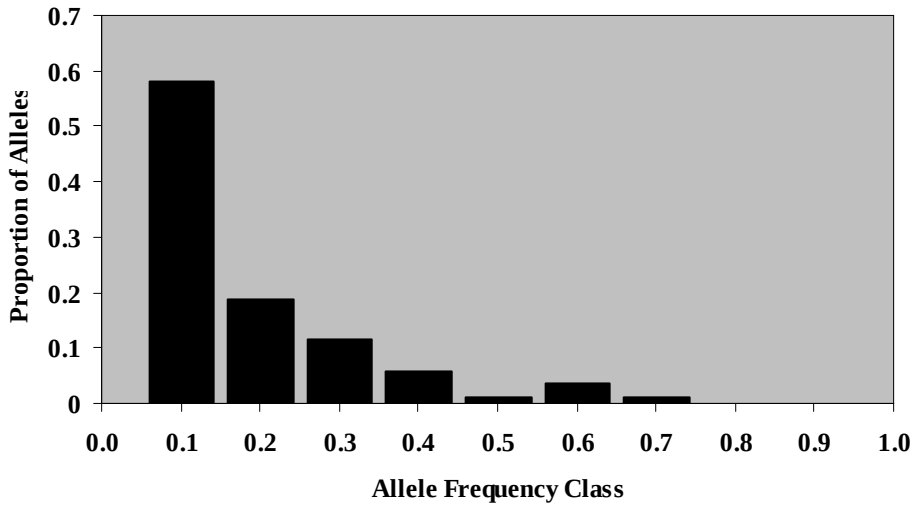

Fig. 2. Allele frequency distribution (mode shift test) for mainland Alaska bowhead whales indicating no apparent bottleneck effect

Table 4. St. Lawrence Island BOTTLENECK data.

	Observed			Under TPM		
Locus	*n*	k_o	H_o	H_e	$(H_o-H_e)/SD$	Probability
TV7	18	8	0.830	0.863	-0.933	0.1848
TV11	20	3	0.653	0.496	1.151	0.1106
TV13	18	5	0.680	0.723	-0.555	0.2525
TV14	20	5	0.758	0.709	0.594	0.3301
TV16	20	4	0.689	0.625	0.604	0.3401
TV17	18	7	0.824	0.828	-0.093	0.4219
TV19	20	4	0.705	0.624	0.756	0.2557
TV20	20	5	0.716	0.710	0.069	0.4473
GATA28	20	7	0.874	0.817	1.144	0.0717
EV1	20	5	0.758	0.710	0.571	0.3418
EV104	20	5	0.805	0.709	1.143	0.0709

n sample size (haploid genomes)
k_o number of alleles observed
H_o observed heterozygosity
H_e expected heterozygosity
SD standard deviation

* Positive $(H_o-H_e)/SD$ values indicate a heterozygosity excess, negative values identify a deficiency

** Significant *p*-values shown in bold ($p \leq 0.05$)

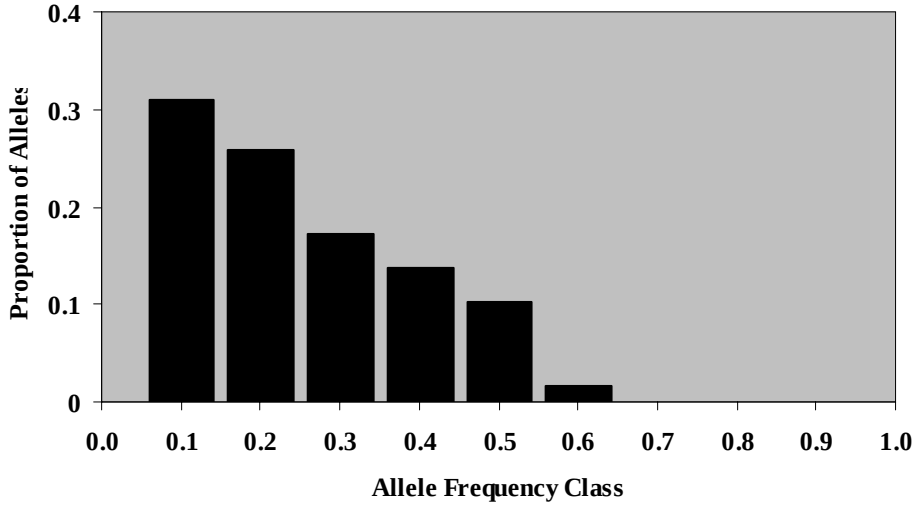

Fig. 3. Allele frequency distribution (mode shift test) for St. Lawrence Island bowhead whales indicating no apparent bottleneck effect.

DISCUSSION

All tests performed are consistent with the conclusion of Rooney et al. (1999a) of no significant genetic bottleneck in the animals sampled in the combined analysis of Alaskan mainland populations. However, with the separation of mainland Alaska and St. Lawrence Island animals, there is evidence of a bottleneck. This separation is based upon migration patterns (Givens et al. 2004). The BCB bowheads winter south of ice flows in the Bering Sea. As ice dissipates, these animals migrate northwards past St. Lawrence Island. Spring hunts on the island occur directly offshore from Gambell on the north and on the south side of the island for Savoonga. Fall hunts for Savoonga occur on the north side. Whales continue the migration passing other whaling villages including Barrow, Alaska where the largest proportion of animals are taken and population estimates are made. It is unclear if whales spend time in the Chukotka, Russia region in the spring. The whales summer in the Beaufort Sea until fall when they head southward again. This migration is more dispersed with whales following the Chukotka, Russia coastline. As St. Lawrence Island animals may follow a different migratory route, they may represent a geographically distinct subpopulation. If so, this group may have experienced a genetic bottleneck that the mainland Alaskan animals were not subjected to.

For the animals sampled at SLI, the Wilcoxon test indicated a significant heterozygosity excess that may be the result of a genetic bottleneck. However, the mode shift test revealed a normal L-shaped distribution for SLI, and the sign test was nonsignificant as well. Therefore, SLI, if it is a distinct sub-stock, might have

experienced a genetic bottleneck but not one as severe as to be detected in most of our analyses. This is consistent with the results of LeDuc and Taylor (2004) who found high gene diversity in the mitochondrial control region for both SLI and the Alaskan mainland population. Nonetheless, the possibility remains that SLI represents a relatively small subpopulation with somewhat reduced levels of genetic variability. It will require additional sampling from this population to determine if my results are accurate or due to sampling error. Samples taken from the harvests of the mainland Alaskan villages appear to represent a genetically robust population.

Visual observations suggest that BCB bowhead whales are a healthy and actively growing population. Burns (1993) described an increasing presence of bowhead whales near St. Lawrence Island. He stated: "Several factors can be identified as contributing to the general increase in whaling success on St. Lawrence Island. A primary one is the steady increase in size of the bowhead population, which has provided increasing opportunity for success and therefore reinforcement of the incentive to whale." The harvest on St. Lawrence Island is unlikely to deplete the population, if it is a distinct population, due to the small number (4.9 per year, 1990-2002) of whales taken from the area (Givens et al. 2004). Given the results of past assessments of BCB bowhead status, such reasoning seems appropriate (Rugh et al. 2003), and all of these findings, including my genetic results, are suggestive of a 'healthy' population.

CONCLUSIONS

This reanalysis of the BCB bowhead whales confirms the findings of Rooney et al. (1999a) that there is no likely bottleneck effect on genetic variability at microsatellite loci. Therefore, it is not probable that the population has experienced a significant genetic bottleneck as a result of commercial whaling in the 19th century. However, Rooney et al. (1999a) did not separately analyze the SLI samples. The Wilcoxon test of the SLI samples indicate the presence of a significant excess of heterozygosity (p = 0.042), but this was not confirmed by the mode shift or sign tests. Therefore, if there is an effect, it is likely small. Given that this analysis is based on such a small sample of SLI whales, these findings should be viewed with caution and reassessed when larger sample sizes are available. George et al. (2004) noted that the recovery of the bowhead whale is probably attributable to several factors including low anthropogenic mortality, a relatively pristine habitat, and a well-managed subsistence hunt. Therefore, based on several lines of evidence and the results presented here, I suggest that management of BCB bowhead whales under the IWC has been quite successful and effective in balancing the opposing forces of conservation and the subsistence harvest of this previously depleted stock of whales.

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APPENDIX I

Bowhead Whale Sample Data

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
03B1	165	167	241	245	81	81	299	299	193	199	174	180
02B8	165	165	245	245	81	83	299	305	193	199	176	180
00B1	165	189	245	245	83	85	301	305	193	203	174	180
00B10	161	165	245	245	81	83	299	305	193	193		
00B11	161	165					295	299	193	199	178	180
00B12	161	161	245	245	81	83	301	305	193	199		
00B2	165	189	241	245	83	83	301	305	195	199		
00B3	161	165	245	245					199	199	178	178
00B4	161	161	245	245	83	83	305	305	197	203	178	178
00B5	161	163			83	83	299	301				
00B6	161	161			79	83	299	299	193	199	176	180
00B7	161	165	243	245	75	81	303	305	199	199	176	176
00B8	165	165			79	81	301	305	193	203		
00B9	161	163							193	193		
01B1	155	165	243	243	83	83	299	299	193	199	178	178
01B10	165	165	243	243	83	85	299	299	199	207	176	178
01B11	161	163	243	245	73	75	299	301	197	199	174	180
01B12	161	165	241	245	81	81	299	305	193	203	180	180
01B13	165	165	243	243	81	81	299	299	201	203	172	180
01B14	165	165	245	245	81	81	299	305	197	207	180	182
01B15	167	181	245	245	81	81	299	305	193	199	174	180
01B16	165	165	245	245	79	83	299	299	193	203	174	180
01B17	161	163	239	245	73	81	305	305	193	205		
01B19	161	161	241	245	81	83	295	299	193	199	178	180
01B2	155	161	245	245	73	73	301	305	193	209	178	180
01B24	159	165					305	305	193	205	176	176

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
01B25	161	165	243	245	79	79	305	305	197	203	180	182
01B26	157	165	245	245			299	301	193	199	176	178
01B27	157	161			81	81	299	305	197	207	176	178
01B3	161	165	239	245	81	83	301	305	193	203	176	178
01B4	161	161	241	245	83	83	305	305	197	199	178	180
01B6	161	161	239	241	83	83	299	305			174	174
01B7	161	161		245	73	73	299	301			178	180
01B8	163	185	243	245	81	81	301	305	199	205	176	180
01B9	161	165	243	245	81	81	295	303	199	201	178	180
01S3	161	171	241	245	81	81	295	299	199	205	178	180
02B1	161	165	243	245			305	305	197	199		
02B10	165	183	243	245	73	81	299	305	197	203	176	178
02B11	155	161	239	245	73	73	299	305	199	199	178	178
02B12	161	161	243	245	73	73	303	305	199	205	174	178
02B13	161	161					305	305	193	207	180	182
02B14	161	165					303	303	193	197	176	180
02B15	161	187	243	245	83	83	305	305	199	205	176	178
02B16	161	161	241	243	81	81	299	307	193	203	178	178
02B17	165	165	241	245	83	83	299	305	193	193	174	178
02B18	161	161	245	245	83	83	295	305	193	211	176	176
02B19	165	189	245	245	81	83	299	305	199	199	178	180
02B2	161	165	245	245	81	83	305	305	197	209	180	180
02B20	161	161	241	243	81	81	305	305	193	193	180	182
02B21	165	189	239	245	81	81	299	305	197	203	178	180
02B22	161	165	245	245	83	83	299	301	193	193	176	178
02B3	161	163	241	247	83	83	305	307	193	199	174	178
02B4	161	165	245	245	83	83	299	303	193	205	176	180
02B5	161	165	243	243	79	83	299	305	193	199	174	174
02B6	165	185	243	245	81	81	305	305	193	199	178	182
02B7	161	165	245	245			299	307	199	209	174	176

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
02B9	161	165	243	245	79	83	295	301	199	203	180	180
03B10	161	161	243	245	81	81	299	299	193	207	182	182
03B2	161	165	243	245	81	81	301	305	197	199	176	176
03B3	161	165	241	241	81	83	299	305	199	199	176	178
03B4	161	165	241	241	81	83	301	305	193	203	172	176
03B5	155	165	243	245	81	81	299	299	193	203	174	178
03B6	161	161	245	245	79	79	299	301	201	203	176	182
03B7	165	165	243	245	81	83	299	299	193	199	178	180
03B8	163	165	241	243	81	81	299	305	193	193	176	178
03B9	165	165	243	245	73	73	299	301	199	205	176	182
1BC97B	161	161	241	241	73	83	301	305				
1BC98B	155	165			81	83	299	299				
2BC98B	161	161					299	299				
97B1	165	165										
98B17	161	161	243	245	83	83	299	305	197	199	176	178
98B6	161	165	243	245	81	81	299	305	193	193	176	180
99B1	161	161	245	247	81	81	299	305	197	211	178	178
99B10	161	165	245	245	83	83	299	303	203	207	174	182
99B14	147	161	241	245	81	83	299	305	193	195	176	180
99B15	161	163	245	245	81	83	301	301	193	193		
99B17	161	165	243	243	83	85	299	301	197	199	174	178
99B18	165	165			83	83	301	301				
99B19	165	165					301	305				
99B2	165	165	241	243	81	81	299	305			178	180
99B20												
99B21												
99B22	161	161										
99B23	165	187	243	243	73	73	301	305	203	207	178	178
99B24	161	161					305	307	199	205		
99B3	161	161	243	243	81	81	299	305	193	193	172	174
92B1	161	165	241	245	81	83	299	299	193	193		

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
92B2	165	165	241	245	83	83	299	299	199	205		
92B3	165	165	241	241	81	81	301	305	199	199	174	174
92B4	165	165	245	245	81	83	299	305	203	205	178	178
92B5	161	165	245	245	81	83	295	299	203	205	176	180
92B6	161	165	245	245	81	81	299	299	199	201	176	178
92B7	161	165			83	83	299	299	193	199	176	176
92B8	161	171			81	83			197	203		
92B9	157	181	245	245	81	83					174	180
95B18	161	161	245	245	83	83	299	305			174	178
95B4	161	165	241	243	73	81	299	305	199	207		
95B9	161	161	245	247	73	83	299	305	199	199		
96B10	155	165	243	245	81	83	301	305	193	201	174	178
96B20	155	165	243	245	73	73	299	301	197	203	178	182
97B3	161	161	245	245	81	81	301	305	197	203	174	178
97B5	161	165	241	243	81	81	301	305	199	199	176	180
97B6	161	161	243	245	83	83	301	305	199	205	174	178
83B1	181	181	243	245	83	83	303	305	193	197	178	180
84B1			245	247	83	83	301	305	203	207	174	176
84B3												
84B4	161	165	243	243	81	83	299	301	199	209	176	182
86B1												
86B2					83	83	299	299				
86B5	165	165	245	245	81	83	299	301	199	203	174	174
86B6	165	165										
86B7	161	165	243	247	83	83	299	299	197	199	176	180
88B9	159	185	241	245	79	79	305	307				
89B2												
89B3												
89B4					83	83						
89B5	161	165	245	245	73	83	299	305	193	199		
89B6	161	165			83	83						

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
90B1	161	161	245	245	81	81	299	301	199	207		
90B10	161	161			81	81	299	299	197	201		
90B2	161	163	243	243	73	83	299	299	199	207	174	180
90B3												
90B7			241	243	83	83	305	305	197	199		
90B8	161	161	245	245	81	81	301	305	199	203	176	178
90B9	161	165	243	243	81	85	301	305	199	199	176	180
92B11	165	189	243	245	83	83	301	305	199	199	176	176
93B10	161	161	245	245	83	83	299	303			176	176
93B11	161	163	245	245	81	83	299	305	203	211		
93B12			245	245	81	83						
93B13			243	245	81	81	301	305				
93B15			243	243	81	83	299	299				
93B16	161	165	245	245	81	81	299	299				
93B2	161	171	241	245	83	83	299	299	203	205	174	176
93B3	161	165	245	245			299	305	193	205	174	180
93B4	161	161	245	245	83	83	305	309	203	203	182	182
93B5			243	245	81	81	299	301			178	178
93B6			245	245	81	81	299	305	205	207	176	180
93B7	161	161	243	245							176	182
93B9	165	165	245	245	83	83	303	305	197	199		
95B1	181	181	243	245	83	83	299	305			180	180
95B13	181	181	245	245	81	83	299	301			180	180
95B17			243	245			299	305				
95B7	161	161					305	305				
95B8	161	163	243	243							176	178
96B1	161	165	245	245			299	305			174	178
96B11	161	163	245	245			305	305			176	182
96B12	161	161	243	245	81	83	305	305	197	199		
96B14	165	165	241	241			299	301			178	182
96B15	161	163	241	245	83	83	299	301			174	178

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
96B16	161	165	243	245	81	83	299	299				
96B17	163	165	241	241	79	81	301	305				
96B18	161	165	245	247	83	83	299	299			174	178
96B19	161	183	245	245	77	83	299	305				
96B2	165	165	241	245	73	73	299	305			174	182
96B21	165	181	241	243	83	83	301	305	199	199	182	182
96B22	161	161	239	245	81	83	299	301	199	199	174	174
96B23	161	161	243	245			301	301	197	203	178	180
96B24	161	161	241	245	73	73	305	309	193	199	174	174
96B3	161	164	241	245			305	309	197	203	174	178
96B4			241	241			299	299	197	199	180	180
96B5	161	163	245	245	81	83	299	299	199	211	174	178
96B6	165	165	241	243	81	83	299	301	199	205	178	178
96B7	155	155	245	245	83	83	305	309	193	201	174	176
96B8	161	165	243	245	83	83	299	301	193	199	176	178
96B9	155	163	243	245	79	81	301	305	199	205	176	178
97B10	161	161	243	245	81	83	299	305	193	199	176	182
97B11	161	187	241	245	81	81	299	301	205	205	178	178
97B12	165	165	245	245			299	305			174	180
97B13	165	165	243	245	83	83	301	305	193	193	176	180
97B15	165	165	245	245	73	73	299	305	193	201	172	180
97B17	159	159	241	245	83	83	299	299	193	199	176	180
97B18	161	161	245	245	81	83	305	305	199	203	176	178
97B19	161	161	245	245	81	81	299	301	199	205	178	180
97B2	161	165	241	245	81	83	301	307	193	199	180	180
97B4	157	181	243	243	83	83	301	305	199	203	178	180
97B7	161	165	243	245	81	81	299	303	201	203	178	180
97B8	183	183	245	245			299	305	203	205	178	182
03G1	165	165	243	245	81	81	299	305	193	199	172	176
96G3	161	163	245	245	81	81	299	299			176	178
96G1	165	165	243	245	81	81	301	305	199	203	178	178

Sample ID	TV 7		TV11		TV18		TV13		TV17		TV19	
02G2	165	165	243	245	85	85	305	307	193	205	176	178
90KK1	181	181			79	79					180	180
86KK2	161	161			81	83						
86KK3			241	245	81	81	299	305				
00KK1	161	161										
00KK2	161	171			79	83	299	307	199	201	174	180
00KK3	161	165	245	245			305	305			174	178
92N-BC-1	157	165	245	245	73	81	305	305	193	199		
03H1	147	165	243	243	81	83	299	299	199	199		
03H2	161	165	243	245	81	83	301	301	193	199	178	180
03H3	157	161	245	245	73	73	299	301	193	201	178	178
96S2	189	193	243	245			305	305	189	193	178	178
96S1			245	245	81	81			193	197	176	178
84S1	161	163			83	83	299	301				
02S2	161	161	241	243			299	305	199	203	180	180
02S4	161	161	241	243			299	305	199	203	180	180
02S3	155	161	241	241	81	83	299	305	193	207	178	180
02S5	155	159	243	245	77	83	299	299	199	199	176	180
84WW1			245	245	83	83	301	305	197	197		
03WW1	155	161	241	247	83	83	299	305	193	201	174	174

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
03B1	168	170	174	174	137	143	97	103	148	154	186	190
02B8	156	156	130	166	135	143	97	101	144	144	184	186
00B1	168	168	162	174			97	97	150	152	186	186
00B10	166	170	115	174	141	143	97	97	144	148	186	186
00B11	156	170					97	97	150	152		
00B12	168	168	130	173	135	141	97	101	146	154	186	190
00B2	156	166	115	130	135	143	95	97	146	148	190	190
00B3	156	166	115	130	135	143	97	101			186	190
00B4	156	156	130	178	135	135	101	101	146	148	190	192
00B5	156	168	130	178	135	143	95	103	144	148	190	192
00B6	156	156	130	130	135	135	97	97	144	146	186	186
00B7	156	168	170	174	135	141	97	97	148	148	186	186
00B8	168	168					97	97				
00B9	166	170										
01B1	156	168	115	115	135	135	93	97	144	150	186	190
01B10	156	156	115	130	135	141	97	101	144	152	186	190
01B11	156	168	115	178	135	135	97	97	144	150	186	190
01B12	156	156	170	174	143	143	95	97	146	148	186	186
01B13	166	168	162	178	135	143	97	101	150	150	190	190
01B14	156	168	166	170	141	143	97	101	144	148	186	186
01B15	156	170	162	162	143	143	101	103	152	152	184	190
01B16	156	170	166	178	135	143	101	103	148	152	186	190
01B17	156	156	115	130	143	147	97	101	144	146	186	190
01B19	156	170	115	115	137	137	103	103	150	152	186	192
01B2	156	168	130	162	143	143	97	99	148	148	186	190
01B24	166	168	115	182	137	141	101	101	152	152	186	190
01B25	156	156	115	173	139	143	97	97	148	150	186	186
01B26	156	156	170	174	143	143	95	97	146	150	186	186
01B27	156	156	158	166	135	137	97	97	144	148	186	186

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
01B3	156	168	115	130	135	141	97	97	148	156	186	192
01B4	156	156	162	178	137	147	97	101	140	148	186	186
01B6	156	170	130	162	135	143	97	101	146	146	186	186
01B7	156	170	115	166	141	143	97	97	150	152	186	186
01B8	156	156	115	174	137	139	97	101	144	148	186	192
01B9	156	168	162	170	141	141	97	101	144	146	190	192
01S3	166	170	115	173	137	143	97	97	142	150	186	186
02B1	156	170	162	174	137	141	97	101	152	154	186	186
02B10	156	170	158	170	143	143	101	101	142	148	186	192
02B11	156	168	115	162	141	143	97	101	154	156	186	190
02B12	156	156	166	170	135	141	97	97	148	152	186	186
02B13	156	156	130	170	135	141	97	97	144	150	186	190
02B14	156	168	130	166	137	143	97	97	144	148	186	190
02B15	156	170	130	130	135	143	97	103	144	152	186	190
02B16	156	168	115	174	141	143	97	97	148	156	186	190
02B17	156	164	115	170	141	143	97	103	144	152	186	190
02B18	156	168	166	174	139	143	103	105	144	144	186	192
02B19	156	170	174	174	139	141	97	101	146	150	186	186
02B2	156	170	166	170	135	143	97	97	146	146	186	186
02B20	156	168	115	174	135	143	97	101	152	160	186	190
02B21	156	156	115	115			97	101	150	150	186	186
02B22	156	156	115	158	135	143	101	103	146	148	186	186
02B3	156	168	130	170	135	143	97	97	144	154	186	186
02B4	156	168	174	174	143	143	97	97	152	156	186	186
02B5	156	170	115	166	141	141	95	97	150	152	186	186
02B6	156	156	115	115			93	93	148	150	186	190
02B7	156	170	162	182	141	143	95	97	152	154	186	190
02B9	168	170	174	178	135	137	101	101	148	148	186	190
03B10	156	166	158	178	135	141	97	103	146	150	186	186
03B2	168	168	166	166	135	137	97	103	144	146	186	186
03B3	156	168	130	130	137	141	97	103	148	160	186	186

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
03B4	164	170	115	130	143	143	95	97	146	152	186	186
03B5	156	156	115	130	135	143	97	97	148	150	186	186
03B6	156	170	173	178	135	143	97	107	144	152	190	190
03B7	168	170	130	162	135	139	101	101	144	144	186	186
03B8	156	164	130	130	135	143	97	101	144	146	186	190
03B9	168	170	173	174	139	143	97	97	144	146	186	186
1BC97B	168	168	115	162	143	143	97	97				
1BC98B	156	164					97	97			186	190
2BC98B							97	97			186	186
97B1												
98B17	156	170	162	170	143	143	93	97			186	190
98B6	156	156	162	166	135	147	97	103			186	190
99B1	168	170	115	166	135	143	93	95			186	186
99B10	156	168	130	162	143	143	101	101			186	190
99B14	168	168	115	162	135	137	97	97			186	186
99B15	156	156	115	174	141	147	97	101	146	152	186	190
99B17	156	164	162	178	141	141	95	97	144	148	186	190
99B18	156	156					97	101			186	186
99B19											186	186
99B2	156	170	115	158	135	141	101	103	148	148	186	190
99B20											186	190
99B21											186	186
99B22											186	190
99B23	156	168	115	158	137	143	97	97	152	152	186	186
99B24	168	170	115	115			95	97	150	152	186	190
99B3	156	164	162	174			97	101			186	186
92B1	156	168	130	170	135	137	101	103	146	148	186	192
92B2	164	170	170	174	141	143	97	97	144	152	186	186
92B3	156	156	115	174			97	101			184	186
92B4	164	168	130	162	135	139	101	101	144	148	186	192
92B5	166	168	115	174	139	143	97	97	144	152	186	186

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
92B6	168	170	115	174	135	139	95	97	148	152	186	186
92B7	156	170	130	162	135	137	95	97	150	150	186	186
92B8	156	156	115	162			97	97	150	152	186	192
92B9	156	168	115	115	141	141	97	97	146	146	186	186
95B18	156	156	162	173	141	141	97	97	150	152	186	186
95B4	156	156	166	174	137	143	97	97	148	150	186	186
95B9	156	170	130	166	143	143	97	101	146	154	186	186
96B10	156	156	115	158	137	141	101	105	150	150	186	190
96B20	156	170	158	174	137	143	101	101	152	154	190	190
97B3	156	170	130	166	135	143	95	97	154	154	186	190
97B5	156	156	115	130	135	143	97	101	150	154	186	186
97B6	168	168	162	174	135	135	101	101	146	148	186	190
83B1	156	170	174	178	135	137	97	97	146	150	186	192
84B1	156	170	115	115	141	143	97	101	152	152	186	190
84B3												
84B4	168	168	130	158	135	141	97	97	144	150	186	186
86B1	170	170										
86B2	156	168					99	103	144	152		
86B5	156	168	130	174			97	101	146	154	186	186
86B6							97	103	146	146	186	186
86B7	166	168	162	170			97	97	146	148	186	186
88B9	156	156	162	166	135	143	97	105	148	156	186	186
89B2									144	152	186	186
89B3												
89B4	156	156	162	170	135	135	101	101	144	150	184	186
89B5			158	173			101	105	148	156	186	186
89B6							97	97			186	186
90B1	168	168	115	173			101	101	144	144	186	186
90B10			158	166					150	152	186	186

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
90B2	156	156	130	130			97	101	146	146	186	186
90B3											186	186
90B7							101	103	146	148	186	190
90B8	156	170	115	158	137	143	93	97	148	152	186	190
90B9	156	170	115	170			101	101	150	152	184	190
92B11	156	156	115	162	135	141	97	101	146	156	186	186
93B10			162	166	143	143			146	146		
93B11	168	168	158	170			97	97	144	146	186	186
93B12	156	156					95	97	144	152	186	186
93B13	156	170	130	178			97	97			186	186
93B15	170	170					97	103			186	186
93B16			166	180			97	97	148	148	186	190
93B2	170	170	115	115	135	139	97	97	146	150	184	190
93B3	168	172	130	162	135	143	101	101	146	150	186	190
93B4	168	170	115	178	137	143	101	101	144	152	186	190
93B5			166	173	143	143	97	103	148	154	190	192
93B6	156	156	115	174	143	143	97	97	148	152	186	190
93B7			115	174	135	143	95	97	152	152	190	190
93B9	156	156	166	173	137	143			144	148	186	190
95B1	156	156	170	170			97	97	150	152	186	186
95B13							97	97			186	190
95B17	168	168					97	101	144	148	186	186
95B7	156	168	115	170					144	156	186	190
95B8	156	156	170	174					144	150	186	190
96B1	168	168	173	173	143	147	95	97	146	146	186	190
96B11	156	168	130	130	141	141	101	101	144	150	186	186
96B12	156	168	130	158	135	143	97	103	144	146	186	186
96B14	168	168	130	178	135	141	97	101	148	152	186	190
96B15	156	168	162	170	143	143	97	103	144	148	186	186
96B16	156	156	115	162	141	143	97	97	148	152	190	190
96B17	156	164	130	173	141	143	101	101	148	148	186	186

Sample ID	TV20		GATA28		EV1		TV14		EV104		TV16	
96B18	156	156	170	173	141	143	97	103	146	148	190	190
96B19	156	156	115	173	137	143	95	105	144	150	186	190
96B2	156	168	115	170	137	141	97	97	146	156	186	186
96B21	156	156	166	174	135	137	97	97	150	150	184	190
96B22	156	168	130	174	141	143	97	97	152	154	186	186
96B23	156	168	115	162	139	143	97	99	146	150	186	186
96B24	170	170	115	166	135	137	97	97	144	150	184	186
96B3	156	164	115	130			97	103	142	146	186	190
96B4	156	168	130	130	141	143	99	101	146	154	186	186
96B5	156	168	130	170	139	143	97	103	144	144	186	186
96B6	168	168	162	174	135	143	97	97	144	146	186	190
96B7	156	168	115	115	143	147	97	103	146	152	186	186
96B8	156	156	130	178	135	137	97	101	150	150	186	190
96B9	156	168	162	170	139	143	97	97	144	146	186	186
97B10	156	156	158	174	143	143	93	97	148	150	186	190
97B11	168	170	115	162	143	143	97	101	146	152	186	190
97B12	156	164	174	174	135	141	97	103	144	152	186	190
97B13	170	170	162	173	143	147	99	99	148	152	186	190
97B15	164	170	130	178	143	143	101	101	152	154	186	190
97B17	156	168	115	170	137	139	97	101	144	146	186	190
97B18	156	164	174	178	141	143	97	101	144	152	186	190
97B19	168	168	158	170	139	143	95	97	144	150	186	186
97B2	156	170	158	162	135	137	95	101	144	148	186	186

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Bickham, J. W., D. D. Hunter, C. W. Matson, R. M. Huebinger, J. C. Patton, J. C. George, and R. Suydam. 2004. Genetic variability of nuclear microsatellite loci in Bering-Chukchi-Beaufort Seas bowhead whales (*Balaena mysticetus*): A test of the genetic bottleneck hypothesis. Report to the International Whaling Commission. SC/56/BRG/18.

CERTIFICATIONS:

International Wildlife Rehabilitation Council, certified wildlife rehabilitator, 2001